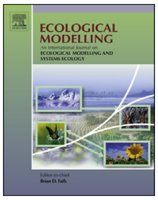
Ecological Modelling 322 (2016) 10–18

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



Incorporating demographic diversity into food web models: Effects on community structure and dynamics

Masami Fujiwara*

Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843-2258, United States

ARTICLE INFO

Article history:
Received 3 September 2015
Received in revised form
20 November 2015
Accepted 25 November 2015

Keywords:
Competition
Diversity
Life history evolution
Predator–prey
Structured population
Trophic interactions

ABSTRACT

Life history strategies affect population dynamics; however, their effects on community dynamics remain poorly understood. A food web model with stage-structured populations (structured food web) and an equivalent model with unstructured populations (unstructured food web) were developed, and their structures and dynamics were compared. Both models incorporated energetic processes and allowed populations to go extinct and invade over time. The results from the two models shared some similarities. For example, all of the initial randomly formed food webs were unstable, but the extinction and invasion rates of populations declined over time. However, there were also clear differences between them. For example, preventing trophic interactions among similar-sized organisms led to a large increase in the number of persisting consumer populations under the unstructured food web, but the number was almost unchanged under the structured food web. Furthermore, an increase in the carrying capacity of primary producers caused an increase in the population extinction rate of consumers under the structured food web, but the extinction rate declined under the unstructured food web. Finally, the average trophic level of consumers in the unstructured food web was often at 2, indicating the food web primarily consisted of herbivores. On the other hand, the average trophic level in the structured food web was significantly higher, indicating the existence of trophic interactions among consumers. These results suggest the importance of incorporating stage structures into food web models to bridge the current theories of food web dynamics and empirical observations because nature consists of structured populations. In particular, I conclude that if one wants to study trophic interactions beyond herbivory, it is crucial to incorporate structured populations into food web models.

1. Introduction

Nature is a full of diversity in terms of their durations of developmental stages, which are defined by survival, reproduction, and developmental rates of individuals in a population (Cole, 1954). This type of diversity is herein termed demographic diversity. Demographic diversity plays an important role in determining population dynamics (e.g. Fujiwara, 2007; Jeppsson and Forslund, 2012; Neubert and Caswell, 2000; Tuljapurkar et al., 2009b), and its importance on community dynamics has been suggested (De Roos et al., 2003; Giacomini et al., 2013; Zhou et al., 2013). For example, Wollrab et al. (2013) demonstrated that a stage-structured predator can promote the diversity of its prey because a bottleneck in the life cycle of the predator can reduce predation pressure on some of its prey, which otherwise may be competitively excluded. Their study demonstrated the potential importance of demographic diversity on population interactions and motivated the current study to investigate how demographic diversity plays a role in determining the structure and dynamics of a food web consisting of a large number of structured populations.

Another set of recent studies also focused on how ontogenetic niche shifts affect food web dynamics (Nakazawa, 2015). Ontogenetic niche shifts occur partly because individuals in a population go through ontogenetic changes in their body size, which affects feeding relationships between consumers and resources (Werner and Gilliam, 1984). For example, Rudolf and Lafferty (2011) argued that a population as a whole may be a generalist, but each life stage within the population may be specialized in a certain resource, making a stage-structured population more vulnerable to resource losses than an unstructured population. This idea has been supported by a series of experimental studies (Rudolf and Rasmussen, 2013a,b). In the current study, the food web model that incorporates ontogenetic niche shifts and demographic diversity of consumers was developed. The model was motivated by the idea that populations can adjust their reproductive values and densities among stages, which can experience different niches, to optimize

---

* Tel.: +1 9798459841; fax: +1 979 845 3786.
E-mail address: fujiwara@tamu.edu

http://dx.doi.org/10.1016/j.ecolmodel.2015.11.015
0304-3800/

their life history strategies for their persistence (Fujiwara et al., 2011).

The current study also fits under a subset of ongoing studies investigating the relationships between species diversity (number of populations of different species) and the properties of ecological communities. Earlier studies argued that species diversity should increase the stability of a community because an increased number of interactions would attenuate population fluctuations reducing the chance of population explosions (Elton, 1927) or an increased number of energetic pathways to consumers would reduce the chance of their population extinction (MacArthur, 1955). On the other hand, a subsequent study using a mathematical model demonstrated that species diversity should reduce stability (May, 1972). Since these pioneering works, numerous studies, both empirical observations (e.g. Cohen et al., 1993; Gross et al., 2014; MacDougall et al., 2013; Martinson et al., 2012; Mora et al., 2011; Winemiller, 1990) and mathematical modeling (e.g. Allesina and Tang, 2012; DeAngelis, 1975; Ives and Carpenter, 2007; Lorrilliere et al., 2012; Otto et al., 2007; Petchey et al., 2008; Yodzis, 2000) were conducted, and these studies have been reviewed by a number of researchers (e.g. Hooper et al., 2005; McCann, 2000; Rooney and McCann, 2012). A majority of recent research has focused on attempting to understand the properties of communities with adapted populations (e.g. Otto et al., 2007; Rooney and McCann, 2012; Rooney et al., 2008) because natural communities are comprised of selected populations (May, 2006; Yodzis, 1981). However, the investigations of the dynamics of randomly assembled communities still continue (e.g. Allesina and Tang, 2012). Therefore, I also investigated how the dynamics of food webs change as they are assembled through a series of population extinctions and invasions.

Here, I investigated the properties of a food web model with stage-structured consumers (hereafter structured model/food web) and an equivalent model with unstructured consumers (hereafter unstructured model/food web). The models were formulated as a system of ordinary differential equations (ODEs), which were treated as semi-continuous time models. The continuous-time formulations allowed the incorporations of individual-level events occurring simultaneously within a population (i.e. birth, death, predation, and development). The discrete-time nature of the models allowed the simple incorporations of population-level events (i.e. extinctions and invasions). The food web models were built as a collection of interacting populations rather than individual-based models; this allowed fast simulations of the models, permitting multiple replications of the model simulations.

2. Methods

The food web models in this study included 10 primary producers and 15 consumers although some of the populations could go extinct (i.e. having a density of 0). The total number of populations was fixed so that the total number of equations in a model remained the same over time. Each of the consumer populations consisted of two stages under the structured food web and a single stage under the unstructured food web. Under both models, primary producers were unstructured (i.e. consisting of a single stage). Consumers fed on primary producers and/or other consumers (collectively referred to as resources), and feeding interactions were determined by the body sizes of potential consumer and resource stages (Fig. 1). The survival of individuals, development among stages, and reproduction were governed by energetic processes. The basic idea behind the energetic model in this study originated from the dynamic energy budget models (Nisbet et al., 2000) although the processes were substantially simplified to accommodate the complexity of food webs. For example, to reduce the number of state variables, the models in this study did not keep track of energy reserve within individuals.

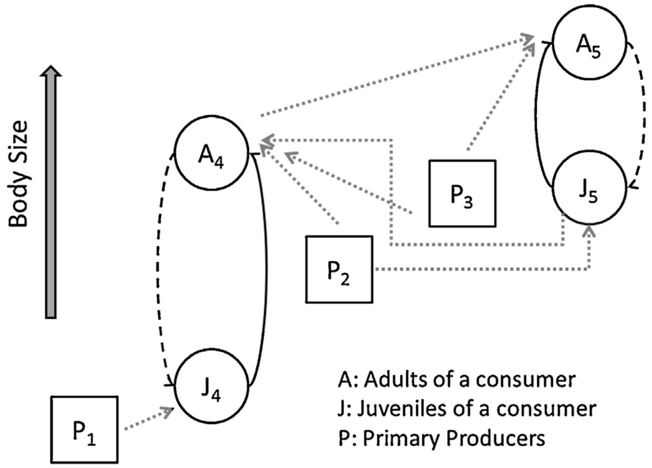


Fig. 1. Conceptual diagram of the structured food web with two consumers and three primary producers. Circles indicate consumers and squares indicate primary producers. Subscripts indicate populations (1–3: primary producers; 4 and 5: consumers). Arrows with solid and dashed lines for consumers indicate development and reproduction, respectively. Arrows with dotted line indicate consumption. As the location of the stage goes up in the figure, the body size increases. For example, P_2 is too large for J_4 to feed on and too small for A_5 to feed on. There is no cannibalism so that there is no feeding interaction between the stages of the same population. This is an example with five populations. In the simulations, there can be up to 10 primary producers and 15 consumers.

A simulation of a model food web begun with populations with randomly selected individual body sizes (traits), but it experienced the extinctions of populations and resettlements of previously extinct populations. Furthermore, consumer populations with new traits (i.e. new species) invaded the system by replacing some of the extinct populations. Consequently, the composition of life history strategies, which were determined by individual body sizes, and the number of persisting populations in the food web changed over time. During this food web assembly process, changes in the properties of the food web were recorded; these properties included the number and biomass of persisting populations, rates of extinctions and invasions, number of population interactions, and mean trophic level of consumers. These properties were compared between the structured and unstructured food webs under five different scenarios that were different in the niche width of consumers (as determined by the range of resource body size that consumers can feed) and the carrying capacity for primary producers.

The food web models included three basic processes: population dynamics, population interactions, and energetics. These processes, along with the algorithm for simulating the models, are described in more detail.

2.1. Population dynamics

A stage-structured consumer population consisted of juvenile and adult stages. Only adults could reproduce, and their offspring were assumed to become juveniles immediately. Individuals in each stage could die from three possible causes: being consumed by others (consumption death), starvation (starvation death), and other natural causes (natural death). Suppose $n_{i,s}$ was the density of individuals in stage i (1: juveniles and 2: adults) of population s, then the dynamic equations were as following:

$$\begin{aligned}\frac{dn_{1,s}}{dt} &= b_s(N,W) - g_s(N,W)n_{1,s} - f_{1,s}(N,W)n_{1,s} - p_{1,s}(N,W)n_{1,s} - mn_{1,s},\\ \frac{dn_{2,s}}{dt} &= g_s(N,W)n_{1,s} - f_{2,s}(N,W)n_{2,s} - p_{2,s}(N,W)n_{2,s} - mn_{2,s},\end{aligned} \qquad (1)$$

where N was a vector of stage densities ($n_{i,s}$), W was a vector of stage-specific individual mass ($w_{i,s}$), $b_s(N, W)$ was a per-population birth rate, $g_s(N, W)$ was a per-capita (per-juvenile) development